STATISTICAL ANALYSIS AND PRESENTATION OF TRINUCLEID (TRILOBITA) FRINGE DATA

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ABSTRACT. The current notation and methods of data presentation for the pits of the trinucleid fringe are reviewed and some shortcomings noted. Using a sample of *Trinucleus fimbriatus* Murchison investigations show that (i) operator errors in selecting half-fringes were negligible, (ii) major features of the pit distribution are not dependent on the size of specimen, (iii) statistically there are no significant differences between the left and right half-fringes, although particular individuals commonly exhibit some asymmetry. It is considered most probable that these conditions hold true in all trinucleids and that numerical studies should be applied throughout taxonomic studies of the group.

SINCE Bancroft (1929) introduced a notation for describing the trinucleid fringe and the use of the fringe characteristics in systematic studies, the taxonomic importance of the pit distribution on the fringe of trinucleids has increased enormously. However, the most favoured system of pit enumeration at the present day is still that proposed by Bancroft (1929, pp. 69–72) and subsequently emended by Whittard (1955, pp. 27–8). That this system has remained unchanged in its essentials since its inception is surprising, as several authors have experienced some difficulties in using it. Williams (1948), in studying the marrolithids of South Wales, found it difficult to apply Bancroft's scheme to the variable numbers of swollen pits typical of these trinucleids. Cave (1957) in a population study of *Salterolithus caractaci* found even Whittard's emended form of notation unsatisfactory to deal adequately with the variation he found within the population. More recently Whittington (1966, pp. 86–90) found a similar degree of variation in *Broeggerolithus nicholsoni* and recognized the need for some new means of documenting the variation present and, while working within the general framework of the traditional notation, presented data on the variation by means of simple histograms rather than attempting to use the standard half-fringe formula. Whittington (1968) again raised the problem of documenting the characteristics of the pit distribution when describing some North American species of *Cryptolithus* where the preservation is such that data are available for complete fringes. In that study he concluded that the full use of Whittard's notation was unnecessary and he concentrated on the number of pits in the complete E_1 arc and the appearance of the inner I arcs, I_3 and I_4, since these three aspects of the fringe pit distribution were the most important for distinguishing the species under consideration. He also (p. 703) raised the problem, often apparently ignored when half-fringe data have been given in the past, that even in such well preserved material the selection of the mid-line of the fringe is often difficult.

The main aim of the present paper is to record the methods and results of an analysis of the distribution of pits on a trinucleid fringe made as a preliminary to the application of statistical techniques in taxonomic studies of the trinucleids. This analysis showed that the half-fringe may in fact be used satisfactorily to represent the characteristics of the whole fringe and that it does not show any dependence on the size of the individual. Although the details of the methods used here were closely linked to one particular

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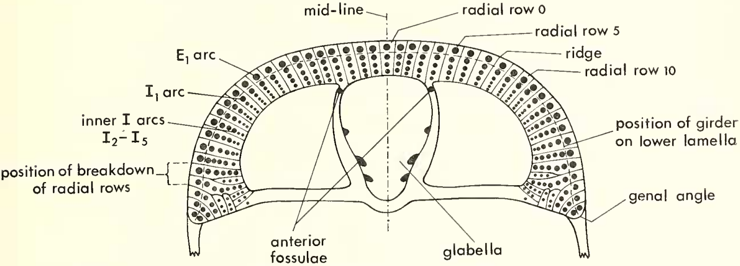
trinucleid, namely *Trinucleus fimbriatus*, this type of approach is, it is believed, applicable to all trinucleid fringes as well as to many problems concerning numerical symmetry and size dependence of morphological features in palaeontological studies. The main purpose of presenting these results here as a separate entity divorced from any accompanying systematic studies is that by so doing it is hoped to be more readily accessible to workers in other fields, for although such techniques as employed here have on occasion been used over the last 30 or 40 years, there is still a need for their much wider application.

The present study was made as a preliminary to the redescription of the trinucleids of the Builth region (Hughes in press) and was carried out entirely independently of Whittington and prior to the appearance of his 1968 paper. It is of interest therefore to note that although the types of material and approaches used were different, the conclusions are basically very similar. The approach adopted here has tended to be more numerical than graphical, for although graphs and histograms of the type used by Whittington are a very useful means of illustration, the purely statistical presentation enables direct objective comparisons to be made between various sets of data; such comparisons are not possible directly from histograms. On the other hand the statistical presentation adopted here could be attacked as being too abstract, and it is believed that in systematic studies the most satisfactory method may well be a conjunct use of both methods, using the graphical aids to illustrate appropriate features. Finally, in this paper the possibilities of extending the results of this study towards a more mathematical approach to the description of the pit distribution of trinucleid fringes are assessed.

As mentioned by Whittington (1968, p. 704) it is chiefly because of the incomplete preservation of the fringe in the bulk of trinucleid material that the vast majority of trinucleid species have been based on half-fringe descriptions, even in species where some complete fringes were known. This reliance on the half-fringe has assumed a symmetrical distribution of the pits of the fringe about the sagittal line—an assumption that has never been put to any real test. Another possible weakness of the traditional 'half-fringe formula' for describing trinucleid fringes is that it has never made any allowance for the possibility that the pit distribution may be dependent on the size of the individual. Although ontogenetic studies (Whittington 1941, pp. 510–11; 1959, pp. 443 ff.) show that the fringe apparently assumes the essential adult characteristics early in the meraspid stage of development, this does not preclude the possibility that there may be some change in the pit distribution with increasing size.

A sample of some three hundred and fifty internal moulds of cephala of *Trinucleus fimbriatus* Murchison 1839 from the black shales of basal Caradoc (*N. gracilis*) age exposed in the middle quarry, Llanfawr, Llandrindod Wells, Radnorshire was collected for this study. This sample consisted of slightly flattened, generally well-preserved, though incomplete remains. Despite the fragmentary nature of many specimens, samples of about 30 were generally obtainable for any particular aspect of the pit distribution. Although these samples were not as large as one could have hoped for, they were, it is believed, sufficient to give adequate data of the fringe characteristics. Apart from the obvious criterion of availability, *Trinucleus fimbriatus* was selected on account of its pit distribution being relatively simple with well-developed radial and concentric elements (see text-fig. 1).

Terminology. The terminology used throughout this study is that in standard use for trinucleids with the exception that Bancroft's term 'concentric row' is replaced by the term 'arc'. This avoids the possibility of confusion which has in the past occurred through some authors abbreviating one or both Bancroft's terms 'concentric row' and 'radial row' to 'row'. It has been found that the standard convention of numbering radial rows and arcs is both useful and generally satisfactory (except where there is a complete lack of radial and concentric arrangement) in defining the various elements of the pit distribution, although as is shown below the continued use of the 'half-fringe formula' should not be encouraged. Throughout this study, symmetry is only considered with respect to the number of pits, not their size or exact relative positioning.



TEXT-FIG. 1. Diagram of *Trinucleus fimbriatus* Murchison showing the distribution of pits on the fringe and the terminology used. The diagram shows radial row 0 and slight asymmetry developed.

STATISTICAL INVESTIGATION

Because of the nature of much trinucleid material it is highly desirable that species should be definable without the necessity of recourse to details of the pit distribution of the full fringe. However, this may only be done if the fringe is symmetrical, or if it is not, any asymmetries must be small enough so as to have no significance. Further, any errors in selecting the mid-line of the fringe must not be significant either. Preliminary observations showed that slight asymmetry of the fringe was common and data were collected to assess the magnitude and characteristics of the asymmetries. In the collection of half-fringe data from material in which the complete fringe is preserved some care must be taken to avoid biasing the data. Such bias may be caused by the systematic misidentification of the mid-line or a personal tendency to select half-fringes showing some atypical feature. In the collection of data therefore one half-fringe only must be included from any one individual and some system should be used for selecting the half-fringe to be considered; in this study left and right half-fringes were selected alternately.

It is seen from Table 1 that of any of the three elements considered, i.e. the E_1, I_1 arcs and the number of radial rows developed, only about one-third of the specimens show symmetrical fringes. If however all three elements are considered simultaneously, then the percentage of bilaterally symmetrical specimens falls to 10%. Thus, although due to the non-perfect preservation it is difficult to consider all elements of the fringe at once, it is clear that perfectly symmetrical fringes rarely, if ever, occur.

As mentioned above it is important to remember that some specimens may show apparent symmetry, or asymmetry, due to the misidentification of the mid-line of the fringe. Thus a specimen having $2n+1$ pits (full-fringe) in a particular arc would appear symmetrical (with regard to that particular arc) if the mid-line were taken along the central radial row, but asymmetrical if taken along either of the adjacent ridges or rows.

TABLE 1. Data giving the number of complete specimens of *Trinucleus fimbriatus* Murchison symmetrical and asymmetrical about the sagittal line with respect to the number of pits in the E_1 and I_1 arcs and the number of radial rows developed.

	E_1	I_1	*Radial rows*
No. of symmetrical specimens	10	9	6
No. of asymmetrical specimens	21	22	16
% of symmetrical specimens	32	29	37

In order to reduce such misidentifications to a minimum the mid-line was taken as passing through the mid-point between the anterior fossulae. Specimens in which this differed markedly from the mid-line as estimated by eye on the glabella, were rejected as being too deformed for symmetry studies, and also for the collection of any precise half-fringe data. Even if small errors due to mid-line misidentification are occasionally included they will, in most cases, be sufficiently rare so as not to have any significant effect on the final outcome, as the two half-fringe pit counts commonly differed by more than one.

In practice the only common case that had to be decided concerning the placing of the mid-line was whether it lay along a radial row of pits (row 0) or along the ridge to one side of that row (which would then be row 1). If there was any systematic error being made in the positioning of the mid-line it could cause a correlation, either positive or negative, between symmetry and the positioning of the mid-line along the row of pits, row 0 or along the ridge on one side. The 2×2 contingency tables given in Table 2 show that no such correlation exists for the E_1 and I_1 arcs considered separately or combined together. Insufficient data are available on the inner I arcs, but the same result is anticipated if such data were available.

Thus it is established that some asymmetry (in the actual numbers and not exact positioning or size of pits) is present in the vast majority of specimens and that this asymmetry is not to be explained by the misidentification of the mid-line of the fringe.

Before considering how much effect these asymmetries may or may not have on the use of half-fringe data it is convenient to investigate on full-fringe data whether there is any correlation between the pit distribution and size of the individual. Since relatively few data were available for arcs internal to I_1, the E_1 and I_1, arcs were again taken as representative of the arc elements of the fringe. Data showing that no correlation with size is present are given in Table 3.

Although relatively few data are available, observations indicate that the major factor that varies in the inner arcs is the row in which the particular arc commences (that is also true in *Cryptolithus tessellatus* (Whittington 1968, pp. 709–10) and in *Bettonia chamberlaini* (Hughes in press). Observations on *Trinucleus fimbriatus* show that this variation only affects the pit counts in the five antero-median rows, data for each half-fringe being given in Table 4, which indicates that this variation is not correlated with the size of specimen. Again in the case of these data small errors may occur due to the misidentification of the mid-line, but since the variation between the rows is small, the effect of any such errors will be insignificant. Any attempt to number the rows from the position of radial breakdown near the genal angles would introduce far greater uncertainties owing to the imprecise way the radial nature of the pits is lost.

TABLE 2. 2×2 tables illustrating the lack of correlation in *Trinucleus fimbriatus* Murchison between the symmetry of the fringe for the E_1 ,I_1 and E_1+I_1 arcs and the development of radial row 0. The value of P gives the probability that inhomogeneities as great or greater than those observed would occur by chance in a random sample drawn from a homogeneous population. Conventionally a value of $P < 0{\cdot}05$ is considered as 'significant', that is, there is a better than 19 in 20 chance that the inhomogeneities observed are truly present in the source population. In this and all other 2×2 tables χ^2 has been calculated by the unadjusted method (see Simpson, Roe, and Lewontin 1960, pp. 189, 322–3). The values of P obtained here by this method never indicate a significant correlation. The adjusted method always errs on the 'safe side' and would never give a significant value for P when the unadjusted method did not. Thus although the samples are small it is considered unnecessary to calculate the more refined adjusted values (in Table 7 cell values of zero are present and so exact probability tests were applied).

	E_1		I_1		E_1+I_1	
Radial row 0	*present*	*absent*	*present*	*absent*	*present*	*absent*
Symmetrical	4	6	4	5	3	5
Asymmetrical	11	10	10	12	11	12*
	$P = 0{\cdot}50$		$P \simeq 1{\cdot}00$		$P = 0{\cdot}70$	

* This figure includes one specimen with a pit of radial row 0 present in the E_1 arc but absent in the I_1 arc.

TABLE 3. 2×2 tables showing the lack of correlation in *Trinucleus fimbriatus* Murchison between the number of pits developed in the E_1 and I_1 arcs and size as measured by the maximum cephalic width (*tr.*), excluding the fringe. For explanation of P see Table 2.

size in mm.	*9–13*	*14–19*
38–42 E_1 pits	13	10
43–47 E_1 pits	5	2
	$P = 0{\cdot}67$	

size in mm.	*9–13*	*14–19*
38–42 I_1 pits	9	14
43–47 I_1 pits	3	3
	$P = 0{\cdot}68$	

Thus it is seen from Tables 3 and 4 that for the E_1 and I_1 arcs and for rows 1–5 of each half-fringe there is no correlation between the number of pits developed and the size of the individual. Although the sample considered only includes a few, probably fairly advanced meraspides, this finding is in general agreement with what has been inferred in the past from ontogenetic studies.

Now that the lack of size correlation has been demonstrated, the problem as to whether the asymmetries in the pit distribution have any significant effect on the use of half-fringe data may be examined. If, as might be expected, the irregularities causing the asymmetries occur randomly on left and right halves of the fringe and are also generally small compared to any inherent variability of the species, then, provided that the data are taken from a random sample of half-fringes, the asymmetry should not affect the final outcome. In order to check this, left and right half-fringe counts were made for the E_1 and I_1 arcs and the data summarized in Table 5.

TABLE 4. 2×2 tables showing the lack of correlation between the number of pits occurring in the radial rows 1–5 of each half-fringe and size in *Trinucleus fimbriatus* Murchison. Size in this table is taken as the maximum width (*tr.*) of the left or right gena. For explanation of P see Table 2.

Row 1

	Left half-fringe			*Right half-fringe*	
Size in mm.	*6–7*	*8–10*	*Size in mm.*	*6–7*	*8–10*
5 pits	4	9	*4–5 pits*	4	14
6 pits	0	2	*6 pits*	0	4
	$P \simeq 1{\cdot}00$			$P \simeq 0{\cdot}56$	

Row 2

	Left half-fringe			*Right half-fringe*	
Size in mm.	*6–7*	*8–10*	*Size in mm.*	*6–7*	*8–10*
5 pits	5	8	*2–5 pits*	5	15
6 pits	1	5	*6 pits*	1	5
	$P \simeq 0{\cdot}60$			$P \simeq 1{\cdot}00$	

Row 3

	Left half-fringe			*Right half-fringe*	
Size in mm.	*6–7*	*8–10*	*Size in mm.*	*5–7*	*8–11*
4–5 pits	5	9	*4–5 pits*	3	13
6 pits	2	9	*6 pits*	4	12
	$P \simeq 0{\cdot}40$			$P \simeq 1{\cdot}00$	

Row 4

	Left half-fringe			*Right half-fringe*	
Size in mm.	*6–7*	*8–11*	*Size in mm.*	*5–7*	*8–11*
3–5 pits	1	7	*3–5 pits*	3	10
6 pits	6	11	*6 pits*	6	16
	$P \simeq 0{\cdot}46$			$P \simeq 1{\cdot}00$	

Row 5

	Left half-fringe			*Right half-fringe*	
Size in mm.	*5–7*	*8–11*	*Size in mm.*	*5–7*	*8–11*
3–5 pits	0	1	*5 pits*	1	2
6–7 pits	6	15	*6–7 pits*	6	20
	$P = 0{\cdot}70$			$P = 1{\cdot}00$	

TABLE 5. Data showing the lack of significant difference between the left and right half-fringe pit counts for the E_1 and I_1 arcs of *Trinucleus fimbriatus* Murchison. For explanation of P see Table 2.

	E_1			I_1		
	mean	*var.*	*n*	*mean*	*var.*	*n*
Left half-fringe	20·70	1·89	55	20·62	1·64	54
Right half-fringe	20·81	1·23	62	20·74	1·35	62
		$P > 0{\cdot}9$			$P > 0{\cdot}9$	

In this and subsequent half-fringe counts, row 0 when present, was taken as having half a pit in each half-fringe. From the data of this table it is seen that for these two arcs there are no significant differences between the two half-fringes. Table 6 gives data comparing the number of pits in the radial rows 1–5, for both half-fringes and again it is seen that there are no significant differences between the two.

TABLE 6. Modes and ranges for the number of pits developed in radial rows 1–5 of both half-fringes of *Trinucleus fimbriatus* Murchison.

	Row 1		
	mode	*range*	*n*
Left half-fringe	5	5–6	15
Right half-fringe	5	4–6	22

	Row 2			Row 3		
	mode	*range*	*n*	*mode*	*range*	*n*
Left half-fringe	5	5–6	18	5	4–6	25
Right half-fringe	5	2–6	26	6	4–6	32

	Row 4			Row 5		
	mode	*range*	*n*	*mode*	*range*	*n*
Left half-fringe	6	3–6	25	6	3–7	22
Right half-fringe	6	3–6	35	6	5–7	29

Table 7, however, shows that the number of radial rows developed is significantly correlated to the number of pits present in the E_1 arc. That is, a specimen having a high E_1 pit count does not have all the extra pits accommodated posterolaterally to enlarge the genal flange where the pit distribution does not show radial arrangement. This correlation indicates that since the E_1 pit counts are not dependent on size, nor do the counts for the two half-fringes show any significant differences, then the same will hold true for the number of radial rows developed and formal tests need not be made.

Thus it has been shown in *Trinucleus fimbriatus* that for the E_1 and I_1 arcs, the numbers of pits in rows 1–5 and the total number of radial rows developed, the half-fringe may be taken as representative of the entire fringe, and it seems reasonable to assume that this

TABLE 7. 2×2 tables showing the significant correlation between the number of pits developed in the E_1 arc in each half-fringe and the number of radial rows present. Since cell values of zero are present exact probability tests were used in place of χ^2 tests.

Left half-fringe

Number of E_1 pits	*18–20*	*21–24*
12–17 rows	19	0
18–20 rows	0	12

$P \simeq 0$

Right half-fringe

Number of E_1 pits	*18–20*	*21–23*
15–17 rows	17	12
18–20 rows	0	11

$P \simeq 0$

should also be true for the other inner arcs and the more laterally placed radial rows (the few data that are available do in fact support this). This is supported by other studies on trinucleids, including *Bettonia* and *Cryptolithus* (Hughes in press), and it seems likely that these general results hold true throughout the Trinucleidae. Although much of this other work on trinucleid fringes has suffered from a similar paucity of data for the inner regions of the fringe, some data on the appearance of the inner arcs (I_3 and I_4) in *Cryptolithus tessellatus* and *Cryptolithus lorettensis* have been presented by Whittington (1968, text-figs. 3–5). Formal tests on his data show that there are no significant differences between the two half-fringes.

Thus the continued use of the half-fringe in trinucleid studies appears to be justified, provided the variation within a population and the asymmetry exhibited by some individuals are borne in mind. Particular caution should be exercised in assessing the significance of the pit distribution when only a few specimens are available, and no new taxa should be erected on slight differences in the distribution of the pits in single specimens or small groups of individuals as has on occasion been done in the past.

In order to facilitate comparisons, it is desirable to have some convention both as to the fringe data selected and as to the manner of their presentation. For the identification of individual pits it is proposed to retain Whittard's notation, but the continued use of the half-fringe formula in specific descriptions cannot be justified, since it cannot express the variation encountered within a species in a manner which enables direct objective comparisons with other samples or species. The data cited will vary in detail from one species to another but they should always be as comprehensive as possible. It is suggested that data for the various arcs and for those radial rows in which variation occurs should always be given. Data for other elements such as the number of radial rows present, distribution of adventitious pits, numbers of pits along the posterior border of the fringe, etc., should be given where appropriate, together with suitable summarizing statistics (see below) and, where useful, illustrated by means of graphical aids such as simple graphs and histograms. In view of the fact that most samples are such that the bulk of the data available are for half-fringes, it is proposed that in order to facilitate comparisons, half-fringe data are given even in cases where the full-fringe data are also available. This ensures that in all data the error sources are, as far as is possible, the same and differing samples are comparable. Although in this study it has been shown that the 'operator variation' due to the misidentification of the mid-line of the fringe has no significant effect, this might not always be the case for all trinucleids, since its magnitude depends on the state of preservation and form of the pit distribution medially as well as the skill of the operator.

The type of summarizing statistics cited will vary depending on the element of the fringe being considered. For elements such as the various arcs where the range in the possible number of pits present is relatively large, continuous variable statistics may be applied, and the mean and variance given. Comparisons between samples may then be made by the use of the 't' test. This test assumes that the distribution does not depart significantly from normality; inspection of distributions obtained shows this condition is satisfied. In elements such as the number of pits in a radial row, where the total number and range is small, continuous variable statistics are not applicable and the mode and range should be quoted. Comparisons between data may then be made with non-parametric tests (see Siegel 1956). In some cases where relatively few data are available summary statistics may be misleading and it would be more satisfactory to present the raw data.

While the above proposals for the description and documentation of the trinucleid fringe are more complex than the half-fringe formulae of Whittard, it is believed that they give a sound basis for the description of any trinucleid fringe, for they are easily adaptable to special features that may be present (e.g. the frontal adventitious pits of *Bettonia*, the data for which may be given or suitable summarizing statistics presented) and to the type and amount of material available. Furthermore it is thought that coupled with some qualitative description and appropriate use of graphical aids a much more comprehensive picture of the distribution and variation of the fringe pits in a population is obtained than could be from the traditional half-fringe formulae.

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